

## RESPONSE OF BIG AND LITTLE BLUESTEM (*ANDROPOGON*) SEEDLINGS TO SOIL AND MOISTURE CONDITIONS<sup>1</sup>

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**ABSTRACT.** Growth responses of *Andropogon gerardi* Vitman (big bluestem) and *A. scoparius* Michx. (little bluestem) seedlings to variable soil type (silt loam vs. clay loam) and soil moisture (dry vs. wet) were examined when individuals were grown in pure and mixed-species cultures. Both species exhibited better growth in more mesic soils (wet and/or clay loam). Dry soil had a significant negative effect on shoot height, shoot production, and total production of *A. gerardi* and resulted in increased root/shoot ratios. Shoot height and shoot production of *A. scoparius* also declined in dry soil, but to a lesser extent. Growth of each species was not significantly different in pure and mixed-species cultures at the density employed in our study (495 plants/m<sup>2</sup>). Our data suggest that in natural prairie communities, interspecific interference between seedlings is relatively unimportant in determining the later distribution of adults. Rather, *A. gerardi* is restricted to mesic lowland sites because of seedling sensitivity to drier conditions; and *A. scoparius* is excluded from these sites through shading by the taller, mature *A. gerardi*. Seedling tolerance to low soil moisture allows *A. scoparius* to colonize xeric upland sites and therefore coexist with *A. gerardi*.

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### INTRODUCTION

Coexistence between closely related species implies an evolutionary divergence with different controlling factors limiting the species populations (Harper et al. 1961). *Andropogon gerardi* Vitman (big bluestem) and *Andropogon scoparius* Michx (little bluestem) are sympatric grasses in the mixed and tall grass prairies of central North America. Weaver (1954) found distinct differences in the microhabitat of the 2 species. *Andropogon scoparius* occurred in greatest abundance in upland regions and was gradually replaced by *A. gerardi* along slopes and in lowlands. Hladek et al.

(1972) observed a similar pattern in *Andropogon* distribution in remnant shale-limestone prairies in Kansas. Lowland sites were characterized by wetter soil conditions and higher soil organic matter. Weaver (1960) demonstrated that in areas with higher annual precipitation, the relative abundance of *A. scoparius* decreased and *A. gerardi* increased.

In an experimental study, Mueller and Weaver (1942) examined the relative drought tolerance of 15 species of prairie grasses grown together. *Andropogon scoparius* seedlings were slightly more drought tolerant than *A. gerardi* under these conditions. They did not, however, examine the species responses when grown separately nor did they exclude interspecific interference (competition and/or allelopathy) as a partial explanation of their results.

Experimentation on seedling growth response may help explain the observed distribution of *A. gerardi* and *A. scoparius* because the seedling stage is critical in

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the establishment of plants (Mueller and Weaver 1942, Harper 1977). In this study we experimentally determined the growth response of *A. gerardi* and *A. scoparius* seedlings to different soil moisture levels, soil types, and species combinations (competitive situations).

## METHODS AND MATERIALS

The experiment was a completely random  $2 \times 2 \times 2$  factorial design with 3 replicates (pots) per treatment combination. The following factors were examined: species composition (pure vs. mixed-species culture), soil moisture (dry vs. wet), and soil type (silt loam vs. clay loam). Each species was grown separately in pure culture (4 seedlings/10 cm diam. pot =  $495/\text{m}^2$ ) and together in mixed-species culture (2 seedlings of each species/pot). This density is similar to the density of prairie grass seedlings ( $376/\text{m}^2$ ) which germinated from soils collected by Weaver and Mueller (1942). Wet soil conditions were created by saturating pots 3 times per week; dry soil was watered to saturation twice per week. Soils were similar in texture, but clay loam had considerably higher nutrient concentration, cation exchange capacity, and percent organic matter than silt loam (table 1).

"Bonilla Big Bluestem" and "Nebraska Native Little Bluestem" seeds were obtained from Wilson Seed Farm, Polk, Nebraska. Seeds were germinated in petri dishes on moistened filter paper and seedlings were randomly assigned to treatments. Pots were placed in the Miami University green house on 22 September 1977. Temperatures ranged from 15-20 C. Fluorescent lighting was used to extend the photoperiod to 12 h.

Growth parameters were measured when plants

TABLE 1  
Composition of soil types used in the experiment.  
Soil texture after Cox (1972).\*

Soil Character	Clay Loam	Silt Loam
Particle size (%)		
> 2 mm	6.1	2.1
sands (2.0 - 0.005 mm)	32.8	12.4
silt (0.05 - 0.002 mm)	34.8	65.7
clay ( $\leq$ 0.002 mm)	32.4	21.9
pH	7.0	6.9
Nutrient concentration (g/m <sup>3</sup> )		
Calcium	7186	2817
Magnesium	1374	344
Potassium	187	134
Phosphorous	99	75
Nitrates (g/m <sup>3</sup> )	250	35
Organic matter (%)	19	2
Cation exchange capacity (meq/100g)	33	12

\*Chemical analyses done by Soil Analysis Division, Ohio Agricultural Research and Development Center, Wooster, OH.

were harvested at the end of 8 weeks (17 November 1977). Shoot height (to the tip of the tallest leaf) of each seedling was measured. Shoots and roots were collected and oven-dried for determination of shoot, root, and total production (shoot + root production) and root/shoot ratio (root production divided by shoot production). Analysis of variance was used to determine significant variables, and Duncan's new multiple range test was used to separate means when significant interactions were found. A critical level of  $\alpha = 0.05$  was used throughout.

TABLE 2  
Regression models of the effects of significant factors on the growth response of  
*Andropogon gerardi* and *Andropogon scoparius* seedlings.

Species and Models <sup>†</sup>	Coefficient of Determination (r <sup>2</sup> )
<i>Andropogon gerardi</i>	
Shoot height = $1.5 + 4.5 M$	0.31
Shoot production = $-2.7 + 7.7 M$	0.35
Total production = $12.1 + 9.9 M$	0.32
Root/shoot = $12.8 - 2.8 M - 3.4 T$	0.43
<i>Andropogon scoparius</i>	
Shoot height = $12.6 + 12.0 M + 12.8 T - 5.6(M \cdot T) - 0.8(T \cdot C)$	0.54
Shoot production = $-4.1 + 3.8 M + 6.0 T$	0.42
Root production = $14.2 - 3.7 T$	0.20
Root/shoot = $2.9 - 1.2 T$	0.41

<sup>†</sup>M = soil moisture, T = soil type, M<sup>\*</sup>T = interaction effect of moisture and soil type, T<sup>\*</sup>C = interaction effect of soil type and species composition.

# RESULTS

Regression models are presented in table 2 to summarize the significant variables for each parameter and show the direction of seedling growth response. In the regressions, a value of 1 was given to pure culture, silt loam, and dry soil. A value of 2 was assigned to mixed-species culture, clay loam, and wet soil. Only factors which were significant according to analysis of variance were placed in the model. No factor significantly affected root production of *A. gerardi* (fig. 1A), or total production of *A. scoparius* (fig. 1B), therefore these models were not developed.

Shoot height, shoot production, and total production of *A. gerardi* seedlings were significantly depressed in dry soil (table 2, fig. 1A). Root/shoot ratios were significantly greater in dry soil and silt loam. Species composition of pots had no apparent effect on any growth parameter of *A. gerardi*.

Shoot height and shoot production of *A. scoparius* seedlings were lower in dry soil, but to a lesser extent than in *A. gerardi* (table 2, fig. 1B). Root production, total production, and root/shoot ratios were not significantly affected by soil moisture differences. Shoot height and shoot production were significantly higher in silt loam. The interaction of soil type and soil moisture had a significant effect on shoot height in *A. scoparius*; shoot height was lowest in dry, silt loam. Although species composition had no apparent main effect, the interaction of species composition and soil type was significant; growth was higher in pure culture using clay loam soils than in mixed-species, silt loam and pure culture, and silt loam.

# DISCUSSION

The observed distribution of a species reflects its responses to abiotic factors and interspecific interactions (Pickett and Bazzaz 1976, Grime 1979). Our data suggest that in the seedling stage, when plants are becoming established, interference between *A. gerardi* and *A. scoparius*

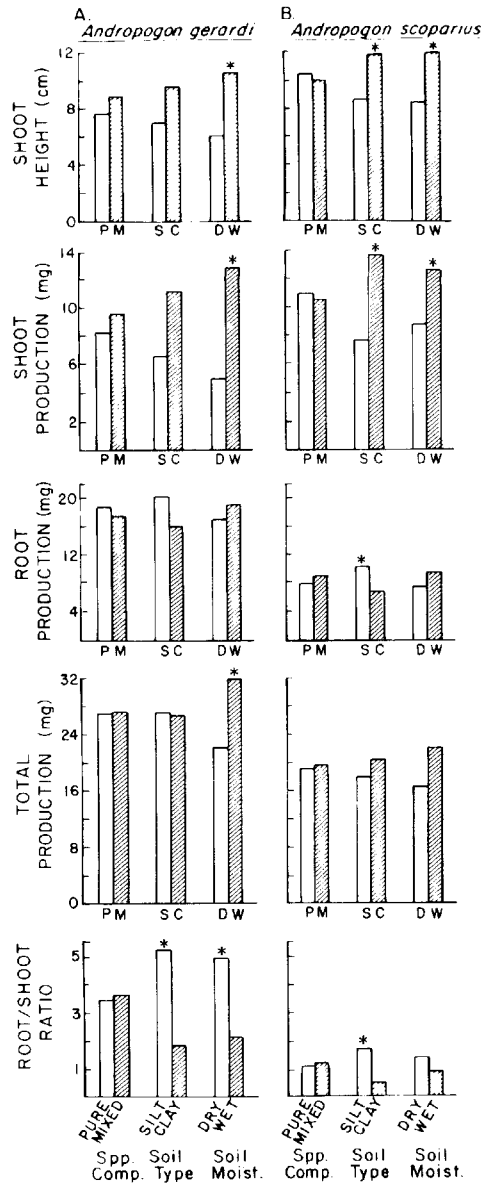


FIGURE 1. Mean growth responses of *Andropogon gerardi* (A) and *Andropogon scoparius* (B) seedlings to experimental levels of species composition, soil type, and soil moisture. Asterisk indicates a significant difference between treatment levels ( $\alpha = 0.05$ ).

is relatively unimportant. Other factors must play a greater role in determining the microhabitats occupied by mature individuals.

Seedlings of both species exhibited better growth under more mesic conditions (wet and/or clay loam soil). *Andropogon gerardi*, however, appeared to be less tolerant of low soil moisture than *A. scoparius*. The dry soil treatment caused a more pronounced depression of *A. gerardi* shoot height, shoot production, and total production and a significantly higher root/shoot ratio. Several authors have suggested that the root/shoot ratio is an important indicator of water stress; higher ratios are attained as water deficit increases (Perino and Risser 1972, Etherington 1975).

Differences in tolerance to more xeric conditions may be due in part to the morphology of the root systems of *A. gerardi* and *A. scoparius*. Weaver and Fitzpatrick (1932) found that *A. gerardi* had a coarse, deep root system which was most efficient under continually moist conditions. In contrast, *A. scoparius* possessed finer, more shallowly penetrating roots which spread laterally, enabling efficient water absorption, even in dry soil.

*Andropogon gerardi* may then be restricted to more mesic sites by greater soil moisture requirements of seedlings. The almost exclusive occurrence of *A. scoparius* in xeric microhabitats is interesting because seedling shoot production was improved under the wet soil treatment of our study.

Although interspecific interference was not apparent between seedlings, other researchers have indicated that it may be important at later stages of growth. Competition for light may be an important factor limiting *A. scoparius* in areas occupied by *A. gerardi*. Weaver and Fitzpatrick (1932) demonstrated that *A. gerardi* seedlings are shade tolerant, but those of *A. scoparius* are not. Once *A. gerardi* becomes established, invasion by upland species (including *A. scoparius*) becomes more difficult because mature *A. gerardi* are as much as 2 m taller (Weaver 1958). Weaver speculated that the absence or scarcity of upland grasses in lowland situations is not due to unfavorable soil conditions,

but to this shading effect. When he removed *A. gerardi* from lowland sites, *A. scoparius* thrived.

Analogous situations have been found in other plant communities. Two sympatric successional annuals replaced each other on a soil moisture gradient (Pickett and Bazzaz 1976). *Abutilon theophrasti* was able to reproduce under all moisture conditions when grown alone. In the presence of *Polygonum pensylvanicum*, however, *Abutilon* reproduced only where water deficit limited the stature of *Polygonum*, or when the *Polygonum* canopy was reduced phenologically. In an English fen, *Glyceria maxima* inhibited the establishment of *Phragmites communis* near open water (Buttery and Lambert 1965). Growth of both species was reduced in drier soil but the greater tolerance of *Phragmites* allowed its establishment in areas devoid of *Glyceria*.

Xeric upland habitats appear to serve as refugia for *A. scoparius* from competition with *A. gerardi*, and can be exploited because of the former species' broader tolerance of soil moisture levels. A niche shift by *A. scoparius* in the presence of *A. gerardi* is substantiated by our data and the removal studies of Weaver (1958). Seedling tolerance to relatively low soil moisture and competition for light appear to be important factors controlling the distribution of mature plants.

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